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Changes in the epiphytic lichen biota of Białowieża Primeval Forest are not explained by climate warming

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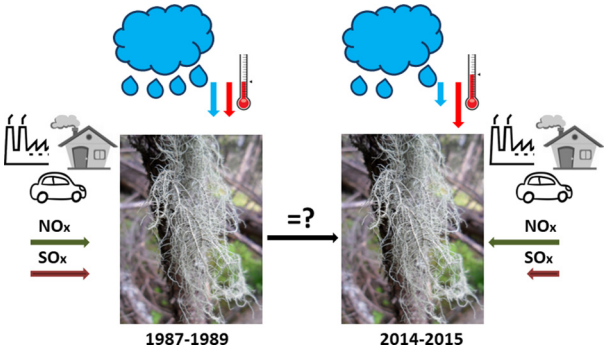
HIGHLIGHTS

- We studied the effect of climate change and pollutants on epiphytic lichens.
- We resampled lichen biota on permanent plots 25 years after original survey.
- We found higher share of nitrogen-demanding lichens, but lower of warm-demanding and high-acidity tolerant lichens.
- The environment of Białowieża Forest reduces impact of global warming on lichens.
- Anthropogenic factors are driving change in lichen biota of natural forest ecosystems.

GRAPHICAL ABSTRACT



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ABSTRACT

Epiphytic lichens are sensitive bioindicators responding to climate change and atmospheric pollutants. Climate warming changes in lichen biota have been reported from Western and Central Europe; therefore, similar trends in the biota of the close-to-natural forests of Eastern Europe were expected. In both examinations (1987–1989 and 2015–2016) of 144 permanent plots the same field method was used. The following functional epiphyte groups were distinguished: climate warming indicators (VDI species and species containing *Trentepohlia* algae) and Wirth's ecological indicators (T – temperature, N – eutrophication, R – reaction, M – moisture). PCA ordination for exploring species composition changes, species richness and diversity (Shannon-Wiener index) in different forest types was used. When compared with the earlier survey, a higher plot species richness, Shannon-Wiener diversity index, and proportion of more nitrogen-demanding lichens, and lower proportions of warm-demanding and high-acidity tolerant lichens were found. No change in the epiphyte biota composition influenced by the decreasing atmospheric precipitation was detected. The species richness and Shannon-Wiener index of climate warming indicators did not show a significant change. Although the share and frequency of epiphytic lichen species and their functional groups changed over a 25-year period, no relationship was found to be related to climate warming: indicators of global warming showed no significant change in frequency, while those with higher value of T even decreased frequency. The changes suggest a connection with eutrophication (increase in frequency of species with higher value of N) and a decrease in sulphur deposition (increase in frequency of species with higher value of R).

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1. Introduction

Climate change is a widely discussed subject, not only in the context of changes in the physical parameters of climate at regional and global levels, but also with regard to changes which it causes to all levels of the living world: individual organisms, their assemblages, and entire ecosystems. The impact of climate change on living organisms is often analysed through resurveys – studies consistent from a methodological point of view, conducted several times in the same area, aimed at capturing changes in species composition, species dominance and frequency. Such studies are criticized because changes in species composition may stem from incompleteness of historical data (e.g. Ellis et al., 2007; Stöckli et al., 2011) and usually unknown workload effort in historical studies (Burg et al., 2015). However, many authors stress that despite these limitations, this is the only technique which allows conclusions not only on changes in assemblages of species, but also in environmental factors (e.g. Kapfer et al., 2017).

Many articles discuss the impact of climate change on various groups of animals, vascular plants and fungi (e.g. Alatalo et al., 2014, 2015; Deluca & King, 2016; Gritsch et al., 2016; Kapfer & Grytnes, 2016; Wiens, 2016; Andrade et al., 2017; Czortek et al., 2018). Those publications describing changes in epiphytic lichen biota concentrate on species growing on the bark of trees (Aptroot & van Herk, 2007; Kirschbaum et al., 2012; Stapper & John, 2015), while those studying rock- and soil-dwelling lichens are rarer (Aptroot & van Herk, 2007; Allen & Lendemer, 2016). Despite the fact that lichens are ubiquitous organisms, their morphological, anatomical and physiological characteristics are extremely vulnerable to any change in their environment and thus they are considered to be one of the most sensitive bioindicators. Climatic conditions, especially temperature and humidity, determine species composition and abundance of lichen biota. These factors are extremely important for lichen biota in many geographical regions, e.g. north-western Italy (Giordani & Incerti, 2008), the north-western United States (Root et al., 2015), and the Netherlands (van Herk et al., 2002). Global change, especially climate warming, is associated, among other things, with an increase in the number of lichens containing *Trentepohlia* algae in the temperate zone (Aptroot & van Herk, 2007; van Herk, 2009). This is due to the particular adaptation of *Trentepohlia* algae to environments with higher temperatures and higher humidity levels. Lichens with these symbiotic algae grow more abundantly in tropical and subtropical areas (Hametner et al., 2014, and the literature cited within). The increase in the species frequency of this functional group of lichens is observed mainly in areas under the influence of humid oceanic climate (Aptroot & van Herk, 2007; van Herk, 2009; Marini et al., 2011), both in forest ecosystems and on solitary exposed trees. At the same time, the loss among macrolichens containing cyanobacteria has also been observed (Rikkinen, 2015; Nascimbene et al., 2016; Rubio-Salcedo et al., 2016). In addition, the climate warming effect is the main cause of the increased presence and frequency of VDI (Verein Deutscher Ingenieure) species – the epiphytic lichen species used in Germany as climate change indicators (VDI 3957 Part 20, 2014 after Stapper & John, 2015). These epiphytic lichens are predominantly thermophilic species, more or less restricted to Western or Central Europe, adapted to humid sites, and sensitive to eutrophication (Wirth, 2010; Stapper & John, 2015).

Not only is climate change responsible for the modification in the species composition of lichen biota; community composition also changes due to increasing or decreasing levels of gaseous (e.g. NO_x, SO_x) and dust emissions discharged into the atmosphere. The changes in lichen biota following the improvement or deterioration of air quality have been reported from many countries (e.g. van Herk, 2009; Łubek, 2010; Adamska, 2011; Hierschläger & Türk, 2012; Kirschbaum et al., 2012; Biazrov, 2013; Klymenko, 2015).

Papers reporting the influence of climate warming on lichen biota in Europe are limited to the western and central parts of the continent (van Herk et al., 2002; Aptroot & van Herk, 2007; van Herk, 2009; Matos et al., 2015; Stapper & John, 2015; Rubio-Salcedo et al., 2016), and only a few lichenological studies have dealt with changes in the lichen biota of forest areas (Aptroot & van Herk, 2007; Marini et al., 2011). In Eastern European countries this phenomenon has not been thoroughly studied so far and therefore we undertook an extensive lichenological survey using a dataset resulting from intensive research carried out in 1987–1989 in Białowieża National Park (NE Poland) (Faliński & Mułenko, 1997). This survey listed many interesting, rare and endangered lichens called "relicts of the primeval (virgin) forest", which are characteristic of natural forests, with minimal anthropogenic influence (Cieśliński & Czyżewska, 1997; Cieśliński et al., 1996). The same area was resurveyed using identical methods and similar workload efforts c. 25 years later (2014–2015). From these data it was possible to analyse the changes in the epiphytic lichen biota and its species composition, with special attention paid to lichens containing *Trentepohlia* photobionts and VDI species reported from Western Europe as climate change indicators. The VDI species, species with *Trentepohlia* algal component and Wirth's indicators analysed in our work were elaborated particularly for Western and Central Europe. However, there are no other specific indicators of lichen characteristics of natural environments (especially for forest areas) that could be used in the assessment of climate warming effect on ecosystems. Wirth's indicators, which provide information about the ecological requirements of lichen species, are also used successfully in Eastern Europe (e.g. Żółkoś et al., 2013; Motiejūnaitė et al., 2014). Bearing in mind that not only climate changes affect the environment and the species composition of the lichen biota, the impact of atmospheric NO_x and SO_x deposition on epiphytic biota was also investigated.

Shifts in the species composition of epiphytic lichen biota in two types of forest communities (deciduous and coniferous) (see Materials and methods section) over the past 25 years were studied in order to determine the importance of climate change in shaping the species composition of epiphytic lichens. To achieve this, a set of ecological Wirth's indicator values (Wirth, 2010) for temperature, moisture, eutrophication (i.e. nitrogen) and reaction (i.e. acidity), and the list of lichen species which are climate warming indicators, i.e. species with *Trentepohlia* algae as a photobiont and VDI species (see Materials and methods section) were evaluated.

Based on the earlier published research (Giordani & Incerti, 2008; Aragón et al., 2012; Root et al., 2015), it was expected that the main factor driving shifts in the species composition of epiphytic lichens would be climate warming (i.e. an increase in temperature and change in precipitation). Therefore, our hypotheses were: (i) the current epiphytic lichen biota (compared to the previous survey) contains a higher proportion of more warm-demanding species (species with higher Wirth's indicator values for temperature, lichens with *Trentepohlia* photobiont and VDI species) (Aptroot & van Herk, 2007; van Herk, 2009; Marini et al., 2011; Stapper & John, 2015) as an effect of the increased mean annual temperature in Białowieża Forest (Malzahn, 2004; Malzahn et al., 2009; Sparks et al., 2009); (ii) the proportion of drought-tolerant epiphytic species increased between the surveys (lower moisture Wirth's value) (compare e.g. Schöb et al., 2008; Sandvik & Odland, 2014) due to the important role played by precipitation in shaping species composition in lichen communities (van Herk et al., 2002; Giordani & Incerti, 2008; Root et al., 2015) and a decrease in annual precipitation in Białowieża Forest (Malzahn, 2004; Malzahn et al., 2009); (iii) the current epiphytic lichen biota contains more species preferring higher nutrient content in the environment (higher value of Wirth's nitrogen indicator corresponding to the nutrients and reaction indicator corresponding to acidity) due to the increased atmospheric nitrogen deposition in the environment (Malzahn, 2004; Malzahn et al., 2009) recognized as one of the effects of global change (Hungate et al., 1997; Hole & Engardt, 2008) and facilitates the recruitment of more nitrogen-demanding species (Purvis et al., 2003; see also: Bobbink et al., 2010; Manninen, 2018).

2. Materials and methods

2.1. Study area

Białowieża Forest is situated in the northeastern part of Poland (52°44′48″N 23°52′15″E) and is the best preserved forest area on the European lowland (Sabatini et al., 2018), as confirmed by its inclusion in the UNESCO List of World Heritage Sites in 2014. This was justified by the very high species richness of plants, animals and fungi, high structural complexity, and the continuity of biological processes over millennia. In the core area of the site trees reach a considerable size and stay in the ecosystem until they die. Dying and dead trees are the source of a large amount of dead wood in varying degrees of decomposition. This substrate is used by numerous animals, fungi and plants, and it is also an excellent water reservoir maintaining the specific microclimate of a forest environment (Pawlaczyk, 2009).

Białowieża National Park (BNP), covering the central part of Białowieża Forest (Fig. 1), protects the oldest parts of the forest, excluded, for the last hundred years, from direct human interference. It contains a wide spectrum of forest communities, diverse in species composition; the age of trees and spatial structure are shaped by natural disturbances, including stand diebacks, insect outbreaks and windthrows. The oldest forests of the BNP stand out against the background of other forests of Poland by their outstandingly high species richness of lichen biota. The high degree of naturalness of these forests stems from the occurrence of many lichen relicts of the primeval forest (Cieśliński et al., 1996; Motiejūnaitė et al., 2004), species very rare in Europe (Kubiak & Łubek, 2016; Kukwa et al., 2017) and some new to science (Guzow-Krzemińska et al., 2016, 2017, 2018; Ertz et al., 2018). The BNP model ecosystems have been shaped for 100 years in undisturbed condition by the natural interplay between different groups of organisms, and have never been severely influenced by human activity or clearcutting. According to palynological studies, Białowieża Forest is unique due to the continuity of the forest cover since the end of the last glaciation (Latałowa et al., 2016). Therefore, it is an excellent object for research, being extremely valuable in a variety of studies, particularly concerning the impact of climate change on ecosystems and organisms, including lichen biota.

2.2. Climate and pollution data

The study area is characterized by a transitional temperate climate, relatively cool, and dominated by continental influences. It is referred to as a forest of subcontinental climate of the temperate zone (Żarnowiecki, 2008). Analysis of the climate over the period 1950–2007 in Białowieża Forest indicates a decrease in the number of days with the minimum air temperatures, while increasing the number of days with the maximum temperatures (Malzahn, 2004; Malzahn et al., 2009). The mean annual temperature of the air is gradually increasing, mainly due to the warmer winter months (Sparks et al., 2009). During the last half-century, the mean annual temperature of the air increased by 1.1 °C (from 6.3 to 7.4 °C). Significant changes are also observed in the amount of precipitation and its annual distribution. In the period 1986–2007 the average annual precipitation amounted to 606 mm, and was over 5% lower compared to the period 1949–1983 (642 mm). The precipitation shows a tendency to increase in winter and summer months, and significantly decreases in spring and autumn months (Malzahn, 2004; Malzahn et al., 2009).

Along with the ongoing process of the drying of habitats and the increase of atmospheric air temperature, an improvement in air quality is observed (Malzahn, 2004; Malzahn et al., 2009). Sulphur deposition, both dry (in gaseous form) and wet (in precipitation), decreased from

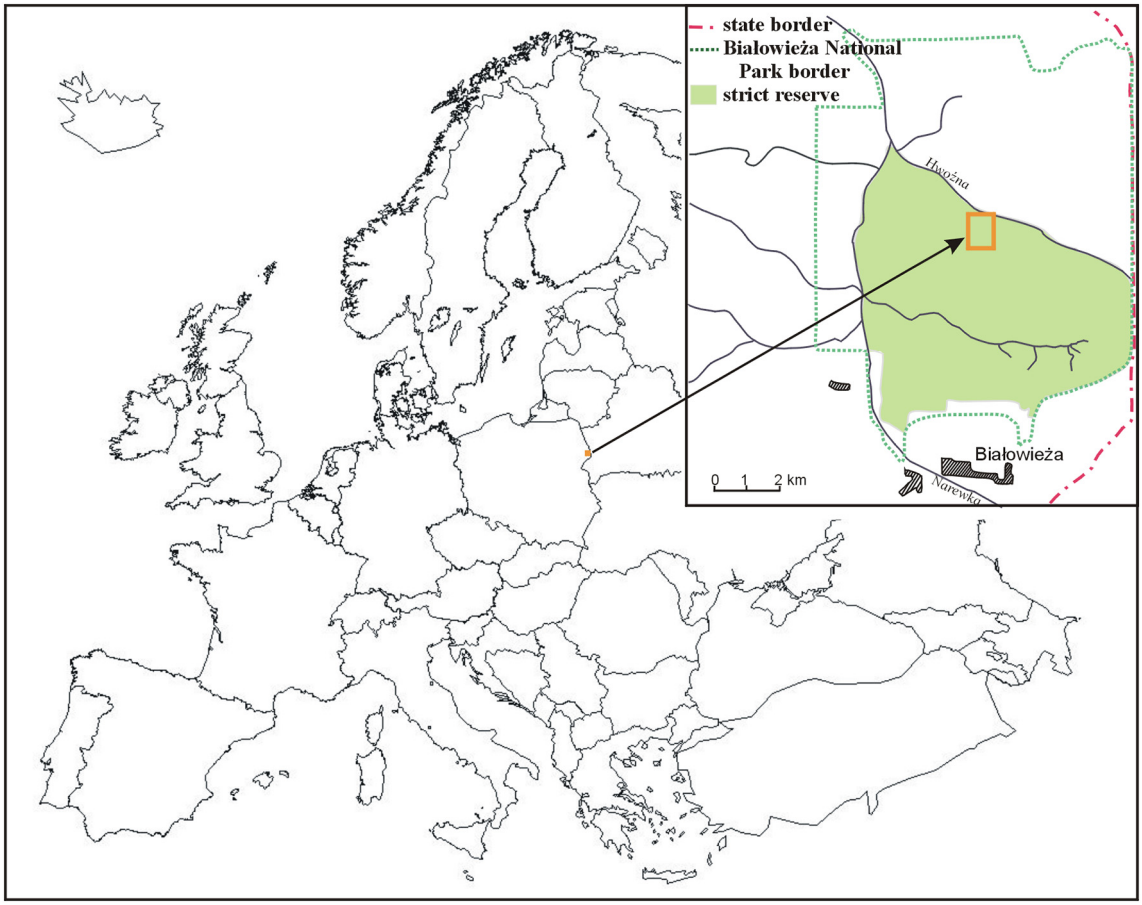

Fig. 1. The study area in Białowieża National Park, NE Poland.

c. 15 kg ha^{-1} year^{-1} (dry deposition) and c. 12 kg ha^{-1} year^{-1} (wet deposition) in 1986 to a mere 1 kg ha^{-1} year^{-1} and c. 6 kg ha^{-1} year^{-1} in 2007, respectively. The present level of total sulphur deposition does not exceed the critical value for the forests of northeastern Europe. In the case of nitrogen, the dry deposition did not change during the period 1986–2007 and fluctuated around the level of 2–3 kg ha^{-1} year^{-1}. The wet deposition of nitrogen in 1986–1995 fluctuated within the range of 7–9 kg ha^{-1} year^{-1} and in 1996–2007 increased slowly, reaching the maximum level of 14 kg ha^{-1} year^{-1} in 2005. The current nitrogen load exceeds the critical value for natural forests (established at a level of 2–5 kg ha^{-1} year^{-1}). This can be considered as one of the factors causing habitat eutrophication in recent years (Malzahn, 2004; Malzahn et al., 2009).

2.3. Study design

The studies were conducted in the BNP on site V-100 (Fig. 1), divided into 144 permanent 100 × 100 m plots (Faliński & Mułenko, 1997). The area is representative for the entire BNP in terms of habitats and the most common forest communities: fertile oak-linden-hornbeam forest *Tilio-Carpinetum* (T-C), streamside alder-ash forest *Circaeo-Alnetum* (C-A), pine-oak mixed forest *Pino-Quercetum* (P-Q), moist oak-spruce forest *Querco-Piceetum* (Q-P), fresh (spruce)-pine forest *Peucedano-Pinetum* (P-P), and black alder bog forest *Carici elongatae-Alnetum* (C.e-A). The epiphytic lichen biota of each forest community is different, due to the diversity of their tree species composition. Cieśliński et al. (1995) reported that the richest lichen biota is characteristic for deciduous forest: T-C, C-A and C.e-A, while that of coniferous forests is much poorer. Due to uncertainties in the phytosociological classification of current forest communities and their delimitation caused by changes in the stands and forest floor vegetation over the years, for our analyses the investigated forests were divided into two functional classes: deciduous (comprising T-C, C-A and C.e-A; 94 plots) and coniferous (P-Q, Q-P and P-P; 50 plots).

The first survey conducted in 1987–1989 (Cieśliński & Czyżewska, 1997) was repeated in 2014–2015 when frequency, as the number of plots on which the species were recorded, was measured. In both surveys the same method was used: in each plot all lichen species (epiphytic, epixylic and epigeic groups) on all available substrates were recorded (Faliński & Mułenko, 1997). A team of two researchers worked on each plot for 3–4 h, investigating all possible microhabitats of lichens. A hand lens with a light was used to identify lichens in the field, and samples for further anatomical and chemical analyses were collected if necessary. The nomenclature of species follows Fałtynowicz & Kossowska (2016). The collected material is deposited in the lichen herbaria of the Jan Kochanowski University in Kielce (KTC) and the University of Gdańsk (UGDA).

Of the 324 lichen species recorded in both (historical and recent) surveys, only 147 were obligatory and facultative epiphytic lichens (Appendix). As epiphytic lichens, we defined those found on the bark of trunks and branches of living trees (European hornbeam *Carpinus betulus* L., small-leaved lime *Tilia cordata* Mill., European ash *Fraxinus excelsior* L., Norway maple *Acer platanoides* L., European white birch *Betula pendula* Roth, European oak *Quercus robur* L., European aspen *Populus tremula* L., European alder *Alnus glutinosa* Gaertn., Norway spruce *Picea abies* (L.) H·Karst and Scots pine *Pinus sylvestris* L., as well as on the bark of trunks of dead trees of the above-mentioned species, and on the bark of stems and branches of living bushes (common hazel *Corylus avellana* L., alder buckthorn *Frangula alnus* Mill., sallow *Salix* sp.) up to 200 cm in height.

All epixylic and epigeic lichens (c. 180 species) were excluded from these analyses, because epiphytic lichens are those most often used as indicators of climate change (e.g. van Herk et al., 2002; Aptroot & van Herk, 2007; Kirschbaum et al., 2012; Stapper & John, 2015). All newly identified epiphytic species, probably present on plots in the past (e.g. *Cetrelia monachorum* (Zahlbr.) W.L. Culb. & C.F. Culb.) but not recognized by previous surveyors due to lack of access to advanced techniques of lichen determination (e.g. thin layer chromatography), were excluded during the analyses. Many species were unknown to earlier investigators as they were described as new to science during the last 20–30 years (e.g. *Biatora pontica* Printzen & Tønsberg, *Lepraria elobata* Tønsberg, *L. jackii* Tønsberg); these too were excluded from the analyses or combined into sensu lato groups according to the classification used 30 years ago (e.g. *Cetrelia cetrarioides* s.l., *Cladonia chlorophaea* s.l., *Lepraria incana* s.l., *Micarea prasina* s.l.). However, it was possible to include some taxa unknown to earlier investigators, due to the revision of specimens collected by them. It revealed that e.g. *Reichlingia leopoldii* during the previous survey was misidentified as *Schismatomma decolorans* (Erichsen) Clauzade & Vězda, or *Lecanora thysanophora* as *Haematomma ochroleucum* (Neck.) J.R. Laundon. Also, the fungus *Microcalicium disseminatum*, often taken into account by lichenologists, was included in analyses.

2.4. Indicator values for lichens

Information on the ecological requirements of epiphytic lichen species (WEIV, Appendix) with respect to certain environmental factors: temperature (T), moisture (M), eutrophication (nitrogen; N) and reaction (acidity; R) were obtained from Wirth (2010). These indicators use a nine-step scale, with 1 being the lowest and 9 the highest degree of the respective environmental factor. For R factors 1 and 9 mean the highest and lowest acidity, respectively (Wirth, 2010). Epiphytic species containing *Trentepohlia* as a photobiont (26 species) and VDI climate change indicators (10 species), according to the VDI Draft Directive (VDI 3957 Part 20, 2014 after Stapper & John, 2015), were used as functional groups for analyses of climate warming (29 species in total, 7 containing *Trentepohlia* photobiont also belonging to VDI species; see also Appendix).

2.5. Statistical methods

A preliminary Detrended Correspondence Analysis (DCA) performed both for deciduous and coniferous forests separately showed relatively low values of gradient length (<3 SD units). Therefore, the PCA ordination was used as the most appropriate method for exploring species composition changes in the lichen biota between the two surveys in both forest types. To perform PCA the *vegan::rda()* function was used. To determine the relationships between the distribution of points representing plots in the PCA ordination space and weighted mean values of Wirth's indicators (T, M, N and R WEIVs), as well as species richness and the Shannon-Wiener diversity index, the *vegan::envfit()* function was used. Thus, the above-mentioned variables as passive vectors were fitted into an ordination space. For each vector, the determination coefficient R^2 and p-value using a permutation test with 999 iterations, and evaluating the significance of results at $p = 0.05$, were calculated. To explore the magnitude of compositional shifts between each historical and resampled plot, the Bray-Curtis compositional dissimilarity index for each type of the forest vegetation was calculated.

To check whether there were changes in the proportion of lichens representing different ecological WEIV requirements for T, M, N and R, as well as to compare the species richness and diversity of lichens (Shannon-Wiener index) over the two sampling periods focusing on the two separate types of the forest (94 replicates for deciduous and 50 for coniferous forest in each sampling period), the paired Wilcoxon test with the maximum level of significance set at $p = 0.05$ was used. The same test was used to determine whether there were changes in species richness and the Shannon-Wiener index of VDI and containing *Trentepohlia* species between the two surveys in each forest type.

To find whether there was a significant change in species frequency (i.e. the number of plots where species occurred in the sampling period) in each type of forest between the two sampling periods, the Chi-squared (χ^2) test with the maximum level of significance set at $p =$

0.05 was used. According to convention, the minimal frequency allowing the use of Chi-squared is five in at least one dataset (McDonald, 2014); however, to focus on the ecological importance of more detailed results, size effects (Nakagawa & Cuthill, 2007) were also included. Therefore, in this procedure species that appeared at least four times, either in the historical or resampled dataset, reducing the tested number of species from 136 to 107 (Appendix) in deciduous, and from 99 to 85 species in coniferous forest, were analysed. Following Moran (2003), the *p*-values corrections (e.g. Bonferroni correction) were not included, since they may lead to overlooking possibly important and interpretable results concerning the high number of species in ecological studies. All analyses were performed using R software (R Core Team, 2018).

3. Results

Principal Component Analysis (PCA), focusing on samples representing coniferous forest communities, explained 44.73% of variance. The main compositional change in the lichen biota in coniferous forests took place along both PCA axes 1 and 2, showing a partial compositional continuum: some points representing historical and recent surveys overlapped in the ordination space (Fig. 2a). The PCA performed for deciduous forest vegetation explained 35.20% of the variance, and showed that the main shift in species composition was along the PCA axis 1 (Fig. 2b). The magnitudes of compositional dissimilarities between the historic and recent surveys, measured by the Bray-Curtis index in both functional types of forest, were similar, namely 0.40 and 0.38 in deciduous and coniferous forests respectively.

In both types of forest resampled species composition was described by high values of vectors representing species richness and the Shannon-Wiener diversity index (Fig. 2a,b, Table 1). Focusing on vectors representing Wirth indicator values for T, M and R, only weak relationships with plots representing shifts in lichen biota in both forest types were found. The only vector which showed a change in its value in association with resampled epiphytic lichen biota in both forest types was N WEIV (Fig. 2a,b, Table 1). In plots representing deciduous forest communities a strong positive correlation was found between vectors representing species richness, the Shannon-Wiener index, and N WEIV (Fig. 2b), whereas in coniferous forests the relationship between those three vectors was relatively weaker. In the coniferous forest type, N WEIV was also correlated positively with T and R WEIVs (Fig. 2a).

Table 1
Parameters of variables passively fitted to the PCA analysis results focusing on forest functional types (coniferous vs. deciduous) with 50 and 94 replications, respectively, for: species richness (Rich), Shannon-Wiener index (Shan) and Wirth's indicators for: temperature (WEIV-T), moisture (WEIV-F), nitrogen (WEIV-N) and reaction (WEIV-R). Determination coefficients R^2 and *p*-values were calculated using a permutation test with 999 iterations.

Parameter	Abbreviation	PC1	PC2	R^2
Deciduous forest				
Species richness	Rich	0.99827	0.05877	0.7986***
Shannon-Wiener index	Shan	0.99438	0.10591	0.7839***
Temperature WEIV	WEIV-T	−0.17557	0.98447	0.7592***
Moisture WEIV	WEIV-F	−0.03443	−0.99941	0.0789**
Nitrogen WEIV	WEIV-N	0.98981	0.14239	0.0875***
Reaction WEIV	WEIV-R	0.14617	0.98926	0.7156***
Coniferous forest				
Species richness	Rich	−0.98654	−0.16353	0.8851***
Shannon-Wiener index	Shan	−0.98325	−0.18224	0.7797***
Temperature WEIV	WEIV-T	−0.79779	0.60293	0.8170***
Moisture WEIV	WEIV-F	−0.95903	0.28331	0.0790*
Nitrogen WEIV	WEIV-N	0.999963	0.02709	0.0871*
Reaction WEIV	WEIV-R	−0.89192	0.45218	0.8686***

Significance of results:
*** $p < 0.001$
** $p < 0.01$
* $p < 0.05$.

In both forest types, in comparison to the historic sampling, significantly higher plot species richness (a change of 14.52 in deciduous, $P < 0.001$ and 9.82 species in coniferous forest type, $P < 0.001$), the Shannon-Wiener diversity index (a change of 0.38 in deciduous, $P < 0.001$ and 0.39 in coniferous forest type, $P < 0.001$), and the proportion of more nitrogen-demanding lichens (higher N WEIV; a change of 0.08 in deciduous, $P < 0.01$ and 0.11 in coniferous forest type, $P < 0.05$) were recorded. The proportion of thermophilic lichens and those with high acidity tolerance was lower recently than historically in deciduous forest (a decrease of T WEIV by 0.05, $P < 0.01$ and an increase of R WEIV by 0.06, $P < 0.01$), whereas in coniferous forests such changes were much weaker. In both types of forest the changes in moisture requirements of lichen biota were not significant between the two sampling periods (Fig. 3). The species richness and the Shannon-Wiener index of VDI species and *Trentepohlia* containing lichens did not show a significant change between historical and resampled data in both coniferous and deciduous forests (Fig. 4).

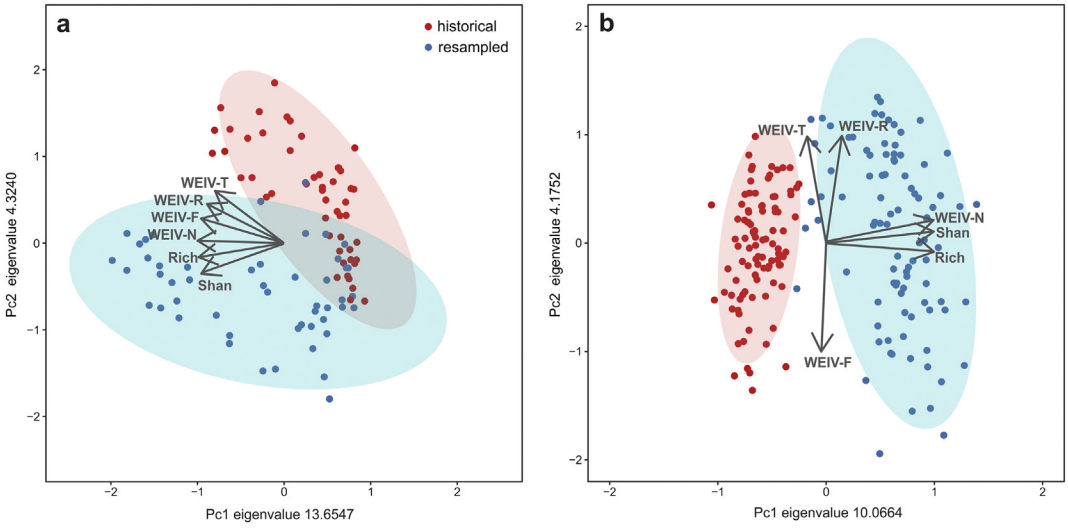

Fig. 2. Results of PCA performed for the species composition of epiphytic lichens surveyed during 1987–1989 and resurveyed during 2014–2015 on plots in: (a) coniferous ($N = 50$) and (b) deciduous forests ($N = 94$). Points represent plots, red and blue backgrounds – ellipses with a 95% confidence level, arrows – environmental variables significantly ($p < 0.05$) correlated with the analyses results (using a permutation test with 999 iterations): Rich – species richness, Shan – Shannon-Wiener diversity index and Wirth's indicators for: temperature (WEIV-T), moisture (WEIV-F), nitrogen (WEIV-N) and reaction (WEIV-R).

Of 107 epiphytes analysed in deciduous forest, 51 species revealed a significant change in frequency between the two time periods (Fig. 5; Appendix). The frequencies of 44 species increased significantly in comparison to historic sampling, the highest shown by *Coenogonium pineti*, *Reichlingia leopoldii*, *Chaenotheca ferruginea*, *Micarea prasina* s.l. and *Microcalicium disseminatum* (changes by: +73, +72, +60, +36 and +56 frequencies, respectively). Twenty species of this group showed concurrent (and in most cases smaller) changes in coniferous forest communities (e.g. *Microcalicium disseminatum*, *Ramalina farinacea* and *Porina aenea*), whereas the remaining species changed their frequencies only in the deciduous communities (e.g. *Cladonia digitata*, *Hypocenomyce scalaris* and *Chaenotheca furfuracea*; changes by: +38, +37 and +31 frequencies, respectively), and the only species which increased its frequency in the case of coniferous forest communities was *Placynthiella icmalea* s.l. (a change by +8 frequencies). Seven lichen species significantly decreased in frequency over the sampling periods, with the highest shifts reported for: *Hypogymnia physodes*, *Pertusaria ophthalmiza* and *Biatora globulosa* (changes by: −27, −11 and −8 frequencies, respectively).

In coniferous forest 21 species (out of 85 analysed) significantly increased in frequency, with the highest shifts in *Lecanora pulicaris*, *Micarea prasina* s.l., *Coenogonium pineti* and *Cladonia macilenta* (changes by: +31, +25, +23 and +22 frequencies). Four species showed a decrease in frequency in coniferous forest: *Usnea dasopoga*, *Cladonia chlorophaea* s.l., *Tuckermanopsis chlorophylla* and *Bryoria implexa* (changes by: −15, −14, −11 and −6 frequencies, respectively).

In both studied types of forest, out of the recorded 29 indicators of climate warming (lichens with *Trentepohlia* algal component or VDI species), 14 showed a significant change in frequency over the period between samplings (Table 2; Fig. 5). In deciduous forests 13 species increased significantly in frequency, e.g. *Anisomeridium biforme*, *Arthothelium ruanum* and *Opegrapha vermicellifera* (changes by: +24, +51 and +42 frequencies, respectively). Six of them showed a concurrent increase in coniferous forests, e.g. *Coenogonium pineti*, *Reichlingia*

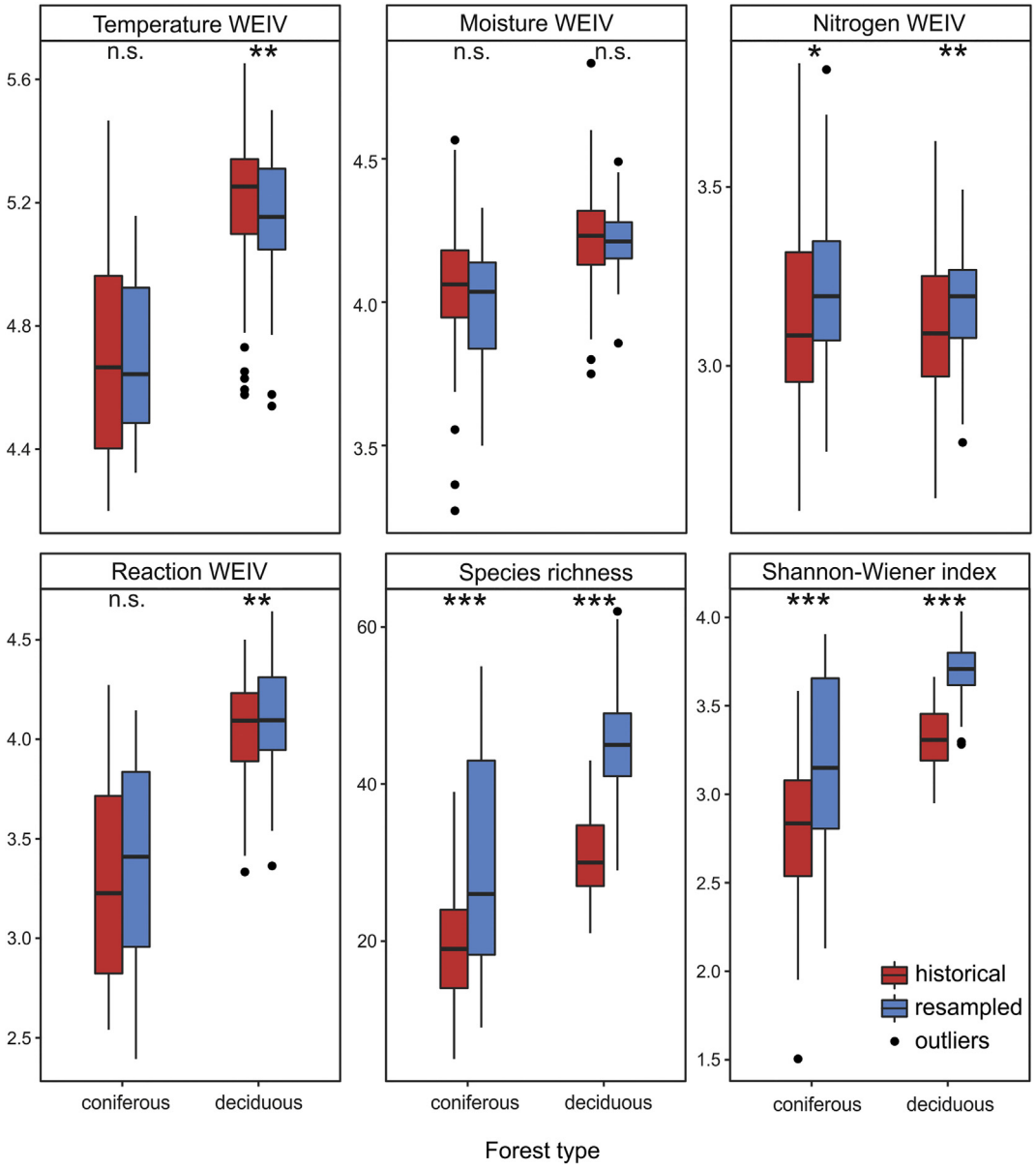

Fig. 3. Comparison of changes in mean values of Wirth's ecological indicators (WEIV), species richness and Shannon-Wiener diversity index between the two periods of lichen sampling (1987–1989 and 2014–2015) performed for deciduous (N = 94) and coniferous (N = 50) forests using the paired Wilcoxon test. The box covers the 95% confidence range. The thick horizontal line is the median. Significance of results: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, n.s. – not significant.

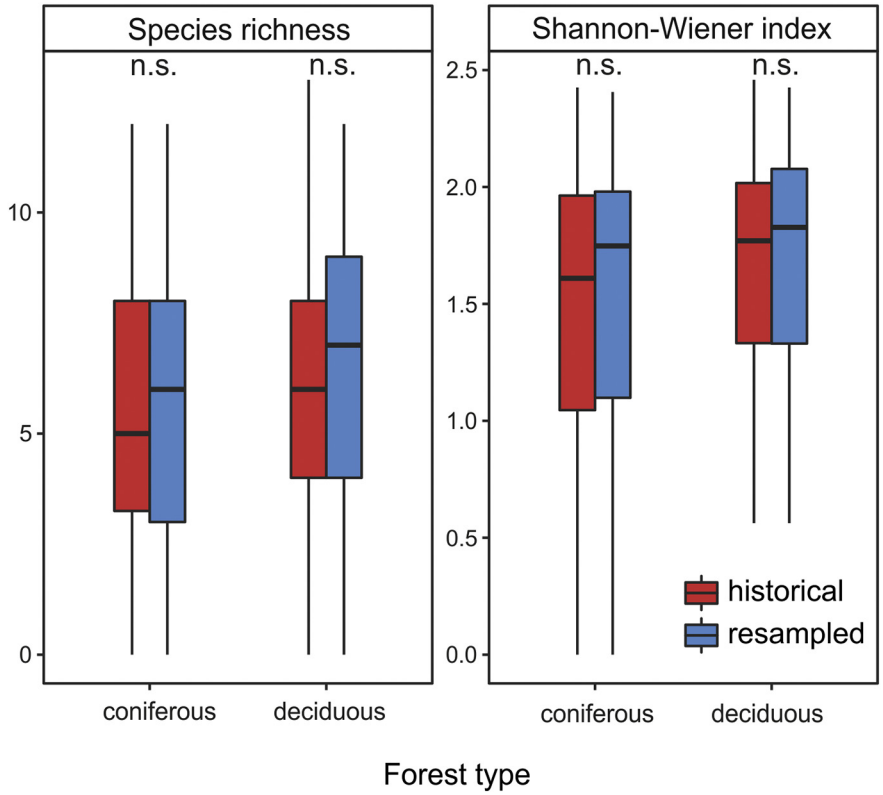

Fig. 4. Comparison of changes in mean species richness and Shannon-Wiener diversity index between the two periods of sampling (1987–1989 and 2014–2015) using the paired Wilcoxon test and performed for deciduous (N = 94) and coniferous (N = 50) forests focusing on 'climate change indicator' species (VDI-species and species containing *Trentepohlia* algae). The box covers the 95% confidence range. The thick horizontal line is the median. Significance of results: n.s. – not significant.

leopoldii and *Porina aenea* (changes by: +23, +13 and +19 frequencies, respectively). Only one climate indicator lichen (*Schismatomma pericleum*) significantly decreased in frequency in deciduous forests between the two sampling events (change by −4 frequencies).

4. Discussion

4.1. Effect of warming

Despite the significant increase of the mean annual temperature of 1.1 °C over the period 1950–2007, no effect of this change on species composition or frequency of epiphytic lichen biota was found. PCA analysis did not show any increase in the share of thermophilic species in either deciduous or coniferous forests. Moreover, the comparison of the historical and recent surveys in deciduous forest even revealed the opposite trend – a significant decrease in the share of thermophilic lichen species (Fig. 3). The frequency of species with high T WEIV ($6 < T < 7$) did not increase, and some of them even decreased in frequency.

The two specialized groups of lichens, the VDI species and species with *Trentepohlia* algae, which are used as climate warming indicators (Aptroot & van Herk, 2007; van Herk, 2009; Stapper & John, 2015), did not show any significant change in species diversity or in the value of the Shannon-Wiener index between the surveys. The frequency of c. 50% of climate warming indicator species (14 out of 29) increased significantly between the two sampling periods. However, a similar share of species (56 out of 113) not considered as climate warming indicators also increased significantly. This suggests that it is not an increase in air temperature but some other factors (e.g. change in pollutant deposition) that caused the observed change in frequency.

Thus, our results are inconsistent with those reported from Western Europe. In the Netherlands, the number and frequency of species with *Trentepohlia* photobionts increased significantly, which was interpreted as an effect of climate warming (van Herk, 2009). Similar trends were reported from German towns (Wetzlar and Giessen), where the number of climate change indicator species increased from 5 to 14 over a period of 5 years (Kirschbaum et al., 2012). An increase in the frequency of VDI species was also reported in lichen biota in Düsseldorf (Germany), where the average number of species per tree at least doubled, while the average number of remaining functional groups of lichens increased only slightly (Stapper & John, 2015). However, it must be stressed that the changes in lichen biota reported from Western Europe were observed in urbanized areas, where in addition to global warming the effect of the urban heat island influenced lichen species composition and richness (compare Munzi et al., 2014; Ohmura & Seaward, 2017). Changes in epiphyte biota were also reported from areas under the strong influence of the Mediterranean climate, where a decrease in the species richness of epiphytic macrolichens with cyanobacteria has been reported (Matos et al., 2015; Rubio-Salcedo et al., 2016). As a result, significant biodiversity loss is expected in the Mediterranean region due to climate change (75% of tested lichen species show tendency to limit their occurrences) and the expansion of Mediterranean species is foreseen (Rubio-Salcedo et al., 2016). Allen & Lendemer (2016) also predicted heavy losses at a level of 93% of the species, among endemic and very rare alpine lichens in the southern Appalachian mountains.

With this background our results are counterintuitive, but they are in line with the experimental studies conducted on an alpine meadow community. There, bryophytes and lichens, both at the functional group and species level, were resistant to different climate change warming simulations (Alatalo et al., 2014). The lack of reaction to global warming is also consistent with trends observed in the species composition of vascular plants of the European forest understorey. Their canopy cover increased due to changes in forest use, game pressure and nitrogen pollution, which in turn decreased light availability on the forest floor (Bernhardt-Römermann et al., 2015). Increased canopy cover reduces the amount of energy reaching not only the forest floor but

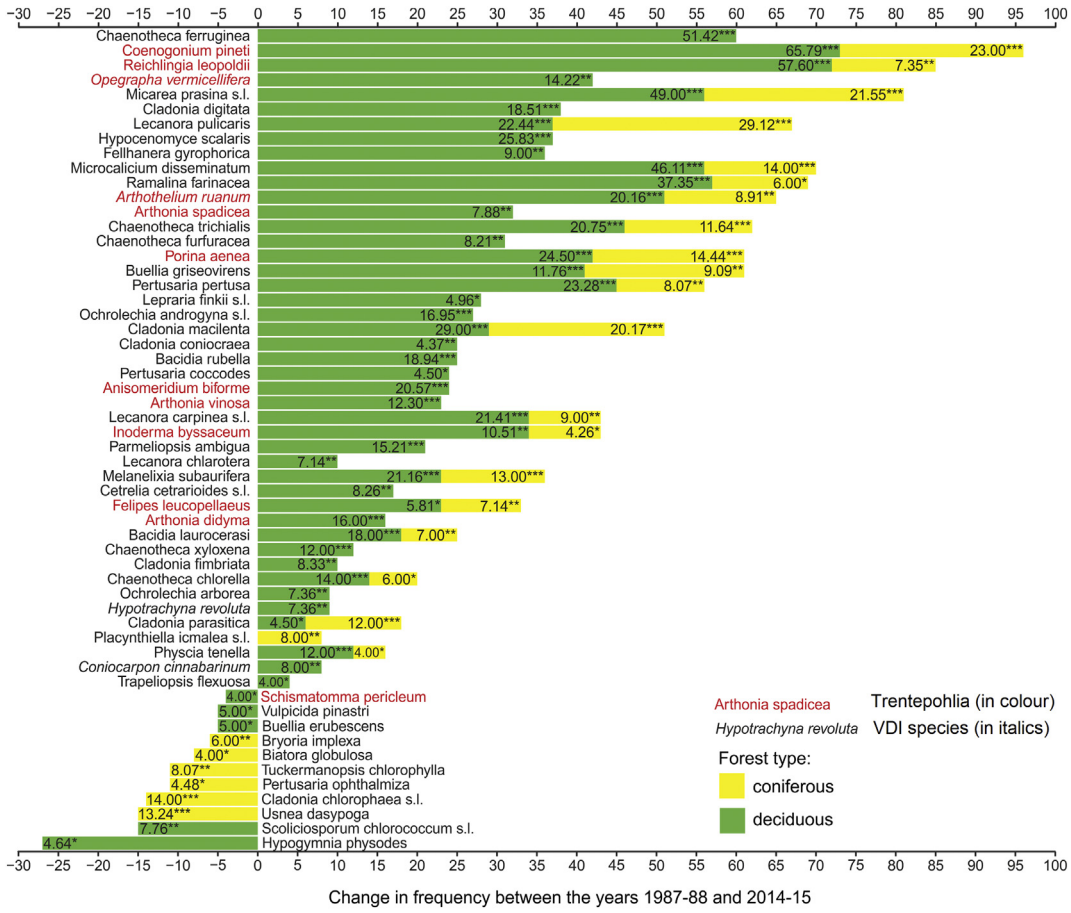

Fig. 5. Significant ($p < 0.05$) changes in the frequency of lichen species between the sampling periods (1987–1989 and 2014–2015) and forest functional types (coniferous vs. deciduous with 50 and 94 replications, respectively). Numbers in the bars are the χ^2-statistics calculated from the Chi-squared test. Significance of results: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

also the base of tree trunks, where many epiphytes grow, slowing down the warming effect.

Aptroot & van Herk (2007) suggested that in closed habitats, especially forests, the response of lichens to global warming is less pronounced. The large size of the forested area of Białowieża Forest (c. 1500 km^2) ensures internal stability, buffering the warming effect despite the regional increase in mean annual temperatures measured outside of the forest canopy. It could also be that the changes in temperature are not yet significant enough to trigger change in the forest biota of lichens. It was also reported that the microclimate formed under the canopy of large forest complexes is a very specific ecological system dependent on many factors, e.g. growth, photosynthesis, regeneration, element cycling, soil formation, biodiversity holding and others (Bussotti & Pollastrini, 2017). The growth of trees and their standing biomass is connected to climate regulation, and is a key parameter allowing evaluation of the ability of forests to mitigate climate change (Bonan, 2008). This was reported for regional and global scales, but it may also have implications on the local scale, especially if large, close to natural forest areas are considered. Ellis (2013) stated that "certain stand types (e.g. old-growth stands) offer greater opportunity for establishment and growth in suboptimal climates, because high microhabitat heterogeneity generates a broader spectrum of microclimatic niches, which buffer an unsuitable macroclimate". Similarly, it was found that the microclimate prevailing in old-growth forested montane regions mitigated climate warming on a local scale (Frey et al., 2016). It is likely that specific microclimate stability in the large and undisturbed Białowieża Forest, with an ecological continuity maintained since the last glaciation (Latałowa et al., 2016), secures the occurrence and continuity of very rare species classed as "indicators of primeval forests", e.g. *Arthonia arthonioides*, *Chaenotheca chlorella* and *Thelotrema lepadinum*.

Marini et al. (2011) support the hypothesis that species richness is positively associated with the availability of high forests (defined as woodlands with natural or/and artificial regeneration and long rotation cycles). High forests provide more stable substrate availability, while young ones, due to high disturbance, low forest continuity and extreme differences in basic environmental parameters (e.g. temperature, humidity, light), are degraded from the point of view of the demands of the majority of lichen species. The positive relationship between lichen species richness and forest age showed that forest structure and microclimate stability are important factors. Aptroot & van Herk (2007) also suggest that some lichens, as epiphytic temperate to boreo-montane species, are not affected by climate change; for example, *Calicium salicinum*, *Evernia prunastri* and *Pertusaria coronata*, common in the BNP, which are characterized by mean T WEIV (the range of value 4–5), mean M WEIV (the range of value 4–5), did not change their frequency. Some authors also suggest that lichens with a green photobiont are less sensitive to climate change (Rubio-Salcedo et al., 2016). This could explain the stability of the epiphytic biota of Białowieża Forest, where lichens with green algae constitute over 90% of the analysed species.

4.2. Effect of change in precipitation

Despite the significant decrease of precipitation recorded in Białowieża Forest during 1986–2007 (Malzahn, 2004; Malzahn et al., 2009), no significant changes in the species composition of epiphytic lichens were noted between the two surveys. This is probably related to the significant specific humidity created and persisting under the canopy of the old natural forest (Frey et al., 2016; Kovács et al., 2017). For this reason, species with a higher moisture index ($6 < M < 7$), e.g.

Table 2
Changes in the frequency of climate-warming indicator species (with *Trentepohlia* algae: "Trent" and VDI lichens: "VDI") focusing on forest functional types (coniferous vs. deciduous with 50 and 94 replications, respectively). χ^2 statistics (calculated from the Chi-squared test) and the level of significance are shown.

Species	Indicator	Deciduous forest		Coniferous forest	
		Change	χ^2	Change	χ^2
Acrocordia gemmata	Trent	1	0.02 n.s.	−1	0.09 n.s.
Alyxoria varia s.l.	Trent	4	0.11 n.s.	−8	2.46 n.s.
Anisomeridium biforme	Trent	24	20.57***	NA	NA
Arthonia arthonioides	Trent	−16	2.33 n.s.	1	0.07 n.s.
Arthonia didyma	Trent	16	16.00***	NA	NA
Arthonia radiata	Trent	4	0.50 n.s.	NA	NA
Arthonia spadicea	Trent	32	7.88**	5	0.71 n.s.
Arthonia vinosa	Trent	23	12.30***	3	0.81 n.s.
Arthothelium ruanum	Trent, VDI	51	20.16***	14	8.91**
Bactrospora dryina	Trent, VDI	−1	0.09 n.s.	NA	NA
Coenogonium pineti	Trent	73	65.79***	23	23.00***
Coniocarpon cinnabarinum	Trent, VDI	8	8.00**	NA	NA
Felipes leucopellaeus	Trent	23	5.81*	10	7.14**
Flavoparmelia caperata	VDI	0	NA	NA	NA
Graphis scripta s.l.	Trent	−1	<0.01 n.s.	11	2.13 n.s.
Hypotrachyna revoluta	VDI	10	7.36**	NA	NA
Inoderma byssaceum	Trent	34	10.51**	9	4.26*
Lecanactis abietina	Trent	3	1.29 n.s.	NA	NA
Opegrapha niveoatra	Trent	−11	0.77 n.s.	4	0.4 n.s.
Opegrapha rufescens	Trent	−6	1.29 n.s.	NA	NA
Opegrapha vermicellifera	Trent, VDI	42	14.22***	7	2.88 n.s.
Porina aenea	Trent	42	24.50***	19	14.44***
Pyrenula nitida	Trent, VDI	2	0.03 n.s.	3	0.39 n.s.
Pyrenula nitidella	Trent, VDI	−5	0.17 n.s.	1	0.04 n.s.
Reichlingia leopoldii	Trent	72	57.60***	13	7.35**
Schismatomma pericleum	Trent	−4	4.00*	NA	NA
Thelotrema lepadinum	Trent, VDI	−4	0.11 n.s.	0	NA
Usnea florida	VDI	6	3.00 n.s.	NA	NA
Zwackhia viridis	Trent	10	0.60 n.s.	8	1.68 n.s.

n.s. – not significant. NA – not applicable.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.00$.

Cetrelia cetrarioides s.l., *Felipes leucopellaeus*, *Ochrolechia androgyna* s.l., are able to currently maintain and even increase their frequency.

4.3. Effect of pollutants

The lichen biota of both deciduous and coniferous forests showed a shift in species composition towards a higher share of species with higher trophic demands, e.g. *Bacidia rubella*, *Melanelixia subaurifera*, and *Physcia tenella* (range of values N WEIV 5–7). In the deciduous forests an increase in the share of species with higher values of the R indicator (lower acidity), e.g. *Arthothelium ruanum*, *Bacidia rubella* and *Melanelixia subaurifera* (R WEIV 5–7) was observed. These changes in species composition, probably related to shifts in the amount of pollutants (NO_x, SO_x) deposited in Białowieża Forest, follow the gradual increase in nitrogen deposition and the resulting eutrophication of the habitats (Malzahn et al., 2009). This is in line with the trends reported in forest floor vascular plants (Bernhardt-Römermann et al., 2015) and epiphytic lichen biota (Root et al., 2015) of Europe. The increase of the frequency of lichen species with higher values of R WEIV could be associated with the increasing pH of precipitation, which was 4.4 in 1994 and 5.3 in 2001 (Malzahn et al., 2009). This change in the R WEIV was significant only in deciduous forests, which is probably due to the higher pH of the bark of most deciduous trees in comparison to the pH of the bark of conifers (Jagodziński et al., 2018). The biota of epiphytic lichens of coniferous trees was not affected by the historical decrease in rain acidity because the bark of conifers is naturally more acidic. The reported pH values of bark of Scots pine in southern Poland was 4.5 (Jagodziński et al., 2018) and 4.0 for Norway spruce in Białowieża Forest (Goldstein, 2011). The pH of most deciduous trees in Białowieża Forest exceeds 5 (e.g. hornbeam, European ash, Norway maple), and only oak and lime bark pH is comparable to conifers (Goldstein, 2011). Therefore, epiphytic lichens, e.g. *Cetrelia cetrarioides* s.l., *Hypotrachyna revoluta*, and *Melanelixia subaurifera*, preferring a closer to neutral pH of the substrate, were unable to develop in the past due to acid rain, and occurred only on single sites in the investigated area (cf. Gilbert, 1986; Gauslaa, 1995). Recently, the epiphytic species of deciduous trees have been spreading owing to the increase in pH of rain water.

5. Conclusions

We did not find any clear sign of climate warming impact on changes in the species composition of the epiphytic lichen biota in Białowieża Forest, which seems to be immune to climate warming, or the change is taking place much more slowly and it is not yet noticeable. However, the share and frequency of lichen species and their functional groups significantly changed over a 25-year period; for example, a significant increase in plot species richness and the Shannon-Wiener diversity index, which could be the effect of a decrease in sulphur and an increase in nitrogen deposition, as well as an effect of the natural process of ecosystem regeneration from the historical traditional use of the forest abandoned close to 100 years ago. Due to the lack of precise local data on temperature and deposition of nitrogen and sulphur, the relationships between those factors and changes in species composition of epiphytic lichen biota were estimated indirectly. All analyses employed Wirth's ecological indicators and species known as climate warming indicators. Our results suggest that future studies on this subject, apart from the impact of climate change, should also include co-occurring changes in the environment, such as pollution or the side effects of changes in land use. There is probably also some observer effect, although it is not possible to measure its influence.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.06.222.

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Author contributions

B.J. and A.Ł. designed the research; A.Ł. and M.K. elaborated the main objectives of the study and collected the data; P.C. collated statistics; P.C. and A.Ł. analysed data; A.Ł. prepared the manuscript, with contributions from the other authors.

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